THE PHYTOGEOGRAPHICAL SIGNIFICANCE OF SNOW MOUNTAIN, NORTH COAST RANGES, CALIFORNIA

L. R. Heckard and J. C. Hickman
Jepson Herbarium, Department of Botany,
University of California, Berkeley 94720

Abstract

Snow Mountain (2152 m), on the Lake-Colusa-Glenn tricounty boundary in northwestern California, is the southernmost peak of the North Coast Ranges to exceed 1900 m. A quarter (128 spp.) of its known flora above 1500 m is at a margin of range there. For 126 of these, Snow Mt. is essentially the southernmost Coast Range locality and, of these 105 are of Sierran affinity. These 128 species are listed, with estimates of numerical importance and summaries of known ranges in California. Distribution patterns and geologic history of montane northern California suggest that many of these species entered the North Coast Ranges from the Klamath Ranges about as early as they occupied the Sierra Nevada and are not necessarily of Sierra Nevadan origin. The small number of Coast Range endemic taxa probably originated in situ from Klamath Region stocks and are now essentially relictual.

In 1893, Katharine Brandegee published a list of 95 taxa characteristic of the Sierra Nevada that had to that date been found in isolated occurrences in the North Coast Ranges. Of these taxa, 84 were reported from the vicinity of Snow Mountain, though most of these records do not appear to be documented by specimens. They resulted from two trips: one by T. S. Brandegee in 1891, the other by K. Brandegee in 1892. Since then there has been almost continuous interest among collectors in the flora of Snow Mt., but no compilation of that flora. The massif is centered nearly on the Lake-Colusa-Glenn tricounty boundary. At lat. 39°23'N (long. 122°45'W) it is the southernmost peak of the North Coast Ranges that exceeds 1900 m (the East Peak reaches 2152 m; the West Peak, 2147 m). To the south, maximum elevations drop off rapidly.

Portions of Snow Mt. have been proposed for Federal Wilderness status for many years, but action is currently at a standstill. The area is one of diverse natural values but most important is its flora. One of us (LRH) first visited Snow Mt. in 1956. Since 1979 we have collaborated on compilation of a florula of the mountain massif above 1500 m, an area of approximately 55 km^2 encompassing an elevational range of 650 m. To date, more than 500 taxa of vascular plants are known from this area, more than a quarter of which are at an extreme margin of their known geographical ranges. The great majority of these are predominantly Sierra Nevadan (abbreviated SN below) or Cascade (C) taxa in California that range west into the

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Klamath Ranges (KR) and thence south, normally spottily and only at higher elevation, through the North Coast Ranges (NCR) to Snow Mt. They may or may not also occur in the Transverse (T) or Peninsular (P) Ranges of southern California. Some have isolated occurrences in the South Coast Ranges (SCR), especially the San Benito and Santa Lucia Ranges. Two taxa are at their northern limit of known distribution on Snow Mt. and a few others are endemic to NCR. Most of those in the last category were described from Snow Mt. material.

This paper reports the phytogeographically interesting taxa known so far from Snow Mt., summarizes their ranges in California, and attempts to assess the vegetational history of the high NCR and the significance of the region for California phytogeography. A paper covering the entire flora is being prepared. In it we present habitat information for all taxa and outline community types.

Perhaps 200,000 specimens from California have been added to herbaria since the completion of Munz' Supplement (1968). Neither Jepson (1925) nor especially Munz (1959, 1968) was able to encompass even the herbarium material available in California when they compiled range descriptions. Range descriptions in floras are not satisfactory for determining currently documented limits of range. To decide whether our Snow Mt. records represent known range limits, we supplemented monographic and floristic literature with examination of about 50,000 herbarium specimens in AHUC, CAS, DAV, DS, JEPS, POM, RSA, and UC. Furthermore, we were given access to the floristic computer files (SLID) at Pacific Union College (PUA) and to data compiled at CHSC and HSC. In several instances the aid of current monographers was enlisted. The list below is not one of "range extensions," but rather of the taxa that make Snow Mt. phytogeographically important. Some of these occurrences have been known and published since the last century, but most are not accounted for by the range descriptions of Jepson (1925) or Munz (1959, 1968).

The North Coast Ranges (NCR) can be distinguished from the more ancient Klamath Ranges (KR) on the basis of geology and topography, and to a lesser extent vegetationally. The predominant substrate of NCR is the Jurassic-Cretaceous Franciscan Complex of sediments and metasediments that have been thrust under continental rocks, the peaks of the range achieving near-current prominence by Miocene. Some peaks of NCR, including Snow Mt., St. John Mt., and the North Yolla Bolly massif, are composed primarily of volcanics and metavolcanics, also of Mesozoic age. By contrast, KR consist of Mesozoic plutonic rocks—igneous and highly metamorphosed substrates including granites and marbles, with a higher proportion of ultrabasic rocks such as serpentine (Jennings 1977). These ranges (KR) make up the oldest continuous land surfaces in

California, having been uplifted by the end of the Mesozoic. The North Coast Range Thrust Fault (South Fork Mountain Fault) divides the two geologic regions. Topographically, this fault essentially follows the valleys of the lower Klamath River and the South Fork of the Trinity River (just east of South Fork Mt.) in the north, arcs east through Stuart Gap just north of the North Yolla Bolly massif, then trends southward, separating the Central Valley from NCR. The narrow band of schistose rocks of South Fork Mountain and adjacent areas are problematical in regional assignment, but now seem most closely allied to NCR rocks (Irwin 1966, Jennings 1977).

Vegetationally, the montane forests of KR differ from those of NCR by the importance in KR of *Tsuga mertensiana* and a more pronounced habitat segregation of *Pinus ponderosa* from *Pseudotsuga menziesii* than occurs in NCR. At lower elevations, mixed evergreen forest in KR characteristically includes *Chrysolepis chrysophylla,* but *Rhododendron macrophyllum* replaces it in equivalent forests in NCR (Küchler 1977).

Few studies of flora or vegetation patterns in higher NCR have been published; Ferlatte's (1974) treatment of the Trinity Alps (KR) is the closest regional flora. Clark (1937) presents a general discussion of vegetation types. Hemphill (1952 Ph.D. diss., Oregon State Univ.) and Keeler-Wolf and Keeler-Wolf (1974 Senior Thesis, Univ. California, Santa Cruz) have completed extensive natural history studies that are not published. Except for Küchler's map (1977), NCR higher montane vegetation is not discussed in Barbour and Major's tome (1977) on the terrestrial vegetation of the state. Snow Mt. is at the southern end of Küchler's (1977) Coast Range Montane Forest, which is approximately equivalent to the Yellow Pine and Red Fir Forests of Munz (1959), the White fir-mixed conifer and Red fir Forests of the Sierra Nevada (Rundel et al. 1977), and the *Abies concolor* and *Abies magnifica* zones of the Klamath Mountains (Sawyer and Thornburgh 1977). Most Snow Mt. taxa are found predominantly or exclusively in the wide diversity of non-forest habitats that occur within these zones. Such habitats include forest openings, serpentine barrens and grasslands, outcrops, screes, rocky flats, and wet meadows.

Geographical subdivisions of the higher NCR are not standardized. Some workers, apparently following Clark (1937), have applied the term Yolla Bolly Mountains to the entire higher NCR but local place names suggest this is inappropriate. We present our scheme in Fig. 1 and summarize it below. Insofar as possible, we have followed names on recent and old maps and have tried to make subdivisions follow natural topographic lines that might reflect habitat barriers to migration.

The northern North Coast Ranges (nNCR: n. and w. of North Yolla Bolly Mts.) are generally too low to support red fir forest or

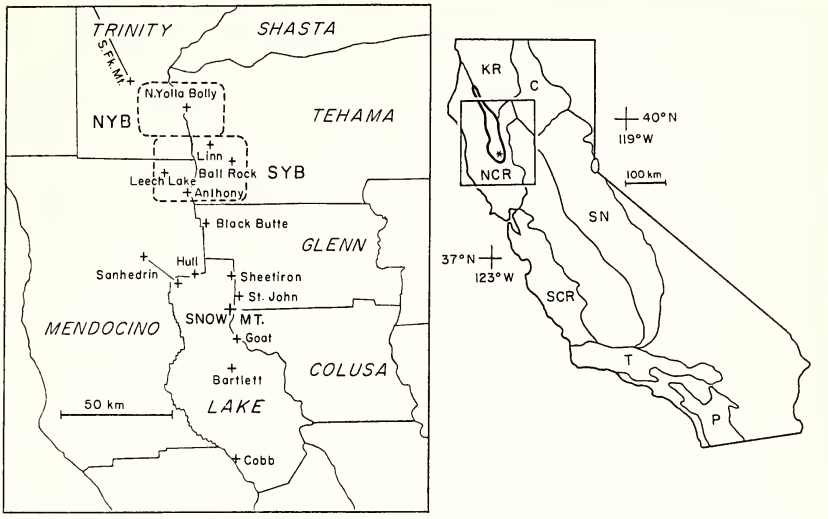

FIG. 1. California mountains and mountain ranges referred to in this paper. C = Cascade Range; KR = Klamath Ranges; NCR = North Coast Ranges (the high NCR are more heavily outlined; "*" indicates the position of Snow Mt.); P = Peninsular Ranges; SCR = South Coast Ranges; SN = Sierra Nevada; T = Transverse Ranges. The enlarged area on the left shows details of the high NCR and lower NCR south of Snow Mt. NYB = North Yolla Bolly Mts.; SYB = South Yolla Bolly Mts.

other upper montane communities, to which the taxa listed here are mostly restricted on Snow Mt. The long ridge of South Fork Mt. encompasses the highest point in nNCR (1850 m); otherwise only the Lassic massif exceeds 1600 m. Both support some high montane communities, but most northwestern California localities from north of the North Yolla Bolly Mts. for these taxa are in KR rather than nNCR.

For our purposes, the North Yolla Bolly Mts. (NYB) include the North Yolla Bolly massif proper (NYB Peak and Black Rock Mt.), Lazyman Butte, and Devil's Hole Ridge south to The Knob. The South Yolla Bolly Mts. (SYB) include Sugarloaf Mt., the SYB massif proper (Harvey Peak, Mt. Linn, Square Lake, Boswell Ridge, and Ovenlid), Ball Rock, Whitlock Camp (Round Mt.), Solomon Peak (the "South Yollo Bolly" of Jepson), Soldier Ridge, Hammerhorn Mt., Buck Rock, Castle Peak, Leech Lake Mt., Government Flat, and Anthony Peak and its southern ridge south to Mendocino Pass at the Tehama-Glenn-Mendocino tricounty boundary.

There are several historically and phytogeographically important collecting localities between SYB and Snow Mt. that will be specified individually in the following treatments. They are more or less isolated from one another and have no inclusive regional name. Pro-

gressively farther south from SYB, they are: Black Butte (2272 m max. elev., Glenn Co., including Keller Lake, Snow Basin, and Plaskett Meadows); Hull (2096 m, including Spruce Grove, Monkey Rock, Windy Gap, Hull Mt. proper, and Boardman Ridge); Sanhedrin (a long ridge including Impassable Rock and Mt. Sanhedrin, Mendocino Co. and Sanhedrin Lookout, Lake Co.); Sheetiron Mt. (1983 m, Lake-Glenn Co. boundary); and St. John Mt. (2057 m, Glenn Co.).

Several peaks south of Snow Mt. in Lake Co. also harbor a few of the taxa considered here and are phytogeographically important in their own rights. We consider that Goat Mt. (1867 m, ca. 13 km south of Snow Mt. on the Lake-Colusa Co. boundary and separated from it by a 1300-m divide) is, in historical/phytogeographical terms, part of the Snow Mt. massif, though we have not studied it as thoroughly and mention occurrences there separately. Farther south in Lake County are Elk Mt. (1206 m), Bartlett Mt. (1476 m), and Cobb Mt. (1440 m). Single known occurrences on these peaks are cited individually below, but two or more documented occurrences from farther south than Goat Mt. served to remove taxa from the select group considered here.

In the list below we give an estimate of numerical importance *on Snow Mt.* for each taxon, using the four relative terms "abundant," "common," "occasional," and "rare." Only taxa that dominate numerically within their general life-form (e.g., trees or small annuals) over a range of habitats were considered "abundant"; "rare" was reserved for taxa known from only one or two populations. Elevational range on Snow Mt. is given, but habitats are mentioned only for plants that are ecologically restricted. The modifier "local" follows numerical importance estimates for taxa with strikingly patchy distributions but little ecological restriction. These data are followed by NCR localities south of Snow Mt. (if any), and then throughout California progressively distant from Snow Mt., using the names and regional abbreviations given above and in Fig. 1. Asterisks indicate taxa listed for Snow Mt. by Brandegee (1893); unless noted, we have confirmed their presence. Nomenclature follows Munz (1959, 1968) except where authorities are cited.

Phytogeographically Important Snow Mt. Plants

**Abies concolor*. Common, above 1550 m, but rarely a strong forest dominant. Also on Goat Mt. and Cobb Mt. Pine Mt. (Lake Co.), St. John Mt., Sheetiron Mt., Sanhedrin, Hull, SYB, NYB, nNCR, KR, C, SN, T, P.

**Abies magnifica* var. *shastensis*. Abundant, the dominant tree above ca. 1800 m, often in mature, even-aged stands. About 10% of

cone scales have non-exserted bracts, a key character for var. *magnifica*. St. John Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR (where it intergrades with *A. procera*), C, SN.

Achillea lanulosa subsp. *lanulosa*. Common, above 1500 m. Sanhedrin, Hull, SYB, NYB, nNCR, KR, C, SN, T, P. Our plants key to *A. millefolium* var. *pacifica* (Rydb.) Jones (Nobs, in Abrams and Ferris, 1960), but have the chromosome number of Nobs' *A. m.* var. *californica* (Poll.) Jeps. ($n = 27$, count courtesy of F. M. Chuang). This offers some support for the preference of some authors (e.g., Tyrl, 1975) to recognize only one taxon of western North American *Achillea*.

Aconitum columbianum. Occasional, 1650–2050 m. Black Butte, SYB, KR, C, SN.

Agrostis thurberiana. Rare, 1900–2000 m. SYB, KR, C, SN, T.

Agrostis variabilis. Rare, 1900–2000 m. Black Butte, SYB, NYB, nNCR, KR, C, SN.

Allium campanulatum. Occasional, scree, 1450–2135 m. Also on Cobb Mt. (*Baker 2222b*), St. John Mt. ("John's Pk.," *Mackie s.n.*, 1902), Hull, Black Butte, SYB, NYB, KR, C, SN, T, P. Disjunct in SCR of Monterey Co.

Alnus incana (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung (=*A. tenuifolia* Nutt.). Occasional, streamsides, 1550–1900 m. Hull, Black Butte, SYB, NYB, KR, C, SN.

**Antennaria argentea*. One collection without elevation (*Brandegee s.n.*, 24 Jun 1891). Reported from Elk Mt. (Brandegee, 1893). Black Butte, SYB, nNCR, KR, C, SN.

Antennaria geyeri. Occasional, scree, above 2000 m. SYB, KR, C, SN.

**Arabis platysperma*. Common, above 1650 m. Hull, Black Butte, SYB, NYB, KR, C, SN, T, P.

Arabis aff. *repanda*. Common, above 1500 m. Black Butte, SYB, KR. True *A. repanda* is known from Nevada Co. s. in (and e. of) SN and in T and P. The undescribed NCR/KR taxon is morphologically distinct and geographically disjunct from it.

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris*. Rare, at 1600 m. Above Alder Springs, Black Butte, KR, C, SN, T. Also at Van Damme State Park, coastal Mendocino Co.

Arceuthobium californicum Hawksworth and Wiens. Rare, on *Pinus lambertiana*, 1640 m. Southwest of Lake Pillsbury, Brush Camp Ridge, Bear Wallow Ridge (reported in Hawksworth and Wiens, 1972), nNCR, KR (reports), C, SN, T, P.

Arctostaphylos nevadensis. Common, near red fir, above 1900 m. Hull, Black Butte, SYB, NYB, nNCR, KR, C, SN.

Arctostaphylos patula subsp. *patula*. Occasional, 1600–1900 m. Also on Goat Mt. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN.

Arenaria congesta var. *congesta.* Occasional, 1700–2135 m. Also on Goat Mt. Hull, Black Butte, SYB, KR, C, SN. Some NCR plants could be considered var. *crassula,* but we believe that var. does not merit recognition.

**Arenaria nuttallii* subsp. *gregaria.* Common, widespread, above 1800 m. Also on Goat Mt. St. John Mt., Sanhedrin, Hull, ne. Mendocino Co., SYB, KR.

**Arnica longifolia* subsp. *myriadenia.* Occasional, wet meadows, above 1950 m. SYB, KR, C, SN. Confused with *A. mollis* in NCR; further taxonomic study of this group is needed.

Aster occidentalis. Occasional, wet meadows, above 1800 m. NYB, nNCR, KR, C, SN.

Astragalus purshii. Rare, 1640 and 1900 m. SYB, KR, C, SN, T. Subspecific limits in this complex species are still not clear. Barneby (1964) considered all NCR plants (and SCR plants, from San Benito Co.) to be var. *tinctus.* To be conservative, our range summary includes the arguably separable var. *lectulus* and var. *longilobus* as well as var. *tinctus.*

Botrychium crenulatum Wagner. Rare, shaded seep, 1680 m (*Howard 2,* JEPS). Recently described (Wagner and Wagner, 1981), this inconspicuous fern is now known from California (Modoc Co. s. through SN to Los Angeles Co.), Oregon, Montana, Utah, and Nevada. This is the first collection from the California Coast Ranges, but it is to be expected wherever appropriate habitats are found (W. H. Wagner, pers. comm. 1982).

**Brickellia greenei.* Common, above 1800 m. Black Butte, SYB, nNCR, KR, C, SN.

Carex aurea. Occasional, 1650–2050 m. Black Butte, SYB, KR, C, SN, T, P.

Carex fracta. Occasional, 1375–2050 m. Also on Bartlett Mt. (*Howell 21013*). Sanhedrin, SYB, NYB, KR, C, SN, T, P.

Carex hoodii. Occasional, 1375–1900 m. Black Butte, SYB, nNCR, KR, C, SN, T, P.

Carex jonesii. Common, wet meadows, above 1925 m. Black Butte, SYB, KR, C, SN, T.

Carex pachystachya. Common, wet meadows, 1600–2000 m. Black Butte, SYB, nNCR, KR, C. Immature material is readily confused with *C. festivella.* One collection of apparently good *C. pachystachya* is known from Sonoma County (*Hoover 5081*).

Carex paucicostata. Occasional, 1650–2050 m. SYB, NYB, KR, C, SN.

Castilleja applegatei var. *fragilis* (Zeile) N. Holmgren. Common, above 1500 m. Sanhedrin, Hull, Sheetiron, SYB, NYB, nNCR, KR, C, SN. Not clearly differentiated from *C. martinii* of the Coast Ranges.

**Ceanothus cordulatus.* Abundant, above 1800 m. Also on Goat Mt. Sanhedrin, Hull, above Alder Springs, SYB, KR, C, SN, T, P.

**Cercocarpus ledifolius.* Occasional, 1525–2050 m, some individuals old and gnarled. St. John Mt., Dicks Butte (ne. Mendocino Co.), KR, C, SN, T, P.

**Chaenactis douglasii* var. *rubricaulis.* Occasional, above 2000 m. Also on Goat Mt. St. John Mt., Sanhedrin, Hull, SYB, KR, C, SN.

Chenopodium incognitum. Rare, ca. 2150 m. Black Butte, SYB, KR, C, SN. *Twisselman 1440* from San Luis Obispo Co. is morphologically distinct but undescribed (fide Wahl annotation, 1955).

Chimaphila umbellata var. *occidentalis.* Occasional, ca. 1600 m. Also on Elk Mt. (*Tracy 2336*). Sanhedrin, Red Mt. (nw. Mendocino Co.), nNCR, KR, C, SN, T, P.

Claytonia chamissoi Ledebour. Occasional, shallow water, 1900–2000 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN, T, P.

Claytonia lanceolata. Rare, collected once (Baker, 1954). Hull, nNCR, KR, C, SN.

Claytonia saxosa Brandegee. Type locality. Occasional, local, above 1650 m. Also on Goat Mt. Sanhedrin, SYB, nNCR, KR.

**Collinsia torreyi.* Occasional, open red fir forest, above 1600 m. Hull, Dicks Butte (ne. Mendocino Co.), Black Butte, SYB, NYB, KR, C. Because of the variability in leaf shape in our plants from lance-ovate to linear-lanceolate we do not recognize var. *latifolia.*

Collinsia wrightii. Occasional, local, 1800–2100 m. Black Butte, SYB, nNCR, KR, C, SN, T.

Cordylanthus viscidus. Rare, yellow pine forest, below 1600 m. SYB, NYB, nNCR, KR, C, SN.

Cornus stolonifera. Occasional, above 1500 m. Black Butte, NYB, KR, C, SN. Taxonomic treatment of Munz (1959) is followed here but *C. stolonifera* and *C. occidentalis* (the latter mostly at lower elevations) are not easily distinguished.

Cryptantha affinis. Common, above 1500 m. Also on Cobb Mt. (*Lummi s.n.,* 1893). Sheetiron Mt., Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

Cynoglossum occidentale. Occasional, above 1500 m. Also on Cobb Mt. (*Dearing et al. s.n.,* 11 Jun 1968). Sanhedrin, Hull, above Alder Springs, SYB, KR, C, SN.

Danthonia unispicata. Occasional, above 1900 m. Black Butte, SYB, KR, C, SN.

Dicentra uniflora. Occasional, ca. 1950 m. Black Butte, nNCR, KR, C, SN.

Dodecatheon jeffreyi subsp. *jeffreyi.* Rare, 1800–1900 m. Black Butte, SYB, NYB, KR, C, SN.

Epilobium ciliatum Raf. subsp. *glandulosum* (Lehm.) Hoch and Raven. Common, above 1800 m. Sanhedrin, Black Butte, SYB, NYB, KR, C, SN, T, P.

Epilobium glaberrimum subsp. *glaberrimum.* Occasional, above 1800 m. Sanhedrin, Black Butte, nNCR, KR, C, SN, T, P.

Epilobium nivium. Type locality. Occasional, rock outcrops, above 1600 m. Also on Goat Mt. St. John Mt., Sheetiron Mt., Castle Peak (SYB of n. Mendocino Co.).

**Eriogonum lobbii.* Occasional, above 1550 m. St. John Mt., Hull, SYB, KR, C, SN.

**Eriogonum spergulinum* var. *reddingianum.* Common, above 1900 m. Hull, Black Butte, SYB, KR, C, SN, T. Disjunct in Santa Lucia Mts., Monterey Co.

**Eriogonum strictum* subsp. *proliferum.* Occasional, 1550–2050 m. Northeast Mendocino Co., SYB, KR, C. Collections of subsp. *proliferum* from the Yolla Bolly Mts. and south have been annotated by Reveal as three separate varieties and as intermediates between these. We see little to be gained from recognizing the varieties created by Reveal (1978), but we suspect the dwarfed serpentine form from NCR and Klamath Mts. deserves taxonomic recognition.

Eriogonum nervulosum (Stokes) Reveal. Type locality. Occasional, above 1975 m. Otherwise known only from: Colusa Co., Frenzl Cr. Botanical Area, fide G. L. Stebbins; Lake Co., Complexion Canyon, *Stebbins 6687*; Cobb Mt. vicinity (Lake-Sonoma Co. line), *Patterson s.n.,* in 1979.

**Eupatorium occidentale.* Occasional, rock outcrops, above 1900 m. Black Butte, SYB, NYB, KR, C, SN.

Fritillaria glauca. Occasional, scree, above 1950 m. Also on Goat Mt. Hull, Black Butte, SYB, nNCR, KR, C (of Oregon).

Galium bifolium. Occasional, moist meadow margins, above 1500 m. Hull, Black Butte, SYB, nNCR, KR, C, SN, T.

**Galium grayanum* Ehrend. Occasional, scree, mostly above 2000 m. Also on Goat Mt. St. John Mt., Hull, Black Butte, SYB, KR, C, SN. Two varieties were recognized by Dempster and Ehrendorfer (1965). Because of their mixed geographic ranges and, on Snow Mt., mixed populations (perhaps even mixed clones), we concur with Dempster and Ehrendorfer (1965, p. 321–322) that their var. *nanum* either is a set of dwarfed forms derived independently from typical *G. grayanum* or is induced by severe environmental conditions. Accordingly, we do not differentiate the two varieties taxonomically.

Galium sparsiflorum subsp. *glabrius* Demp. & Steb. Occasional,

1500–1900 m. Also on Trough Spring Ridge, se. of Snow Mt. (*Chisaki 1166A*). St. John Mt., above Alder Springs, KR, C.

**Gayophytum diffusum* subsp. *parviflorum.* Abundant, above 1500 m. Sheetiron Mt., Hull, above Alder Springs, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P. Some populations have petal and anther size within the range of the outbreeding subsp. *diffusum* as defined by Lewis and Szweykowski (1964) but the stigma is like that of subsp. *parviflorum.*

Gayophytum heterozygum. Rare, ca. 1900 m. Sanhedrin, above Alder Springs, SYB, nNCR, KR, C, SN, T, P. Also disjunct in Monterey and San Luis Obispo Cos.

Hackelia amethystina. Common, above 1500 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR, C, SN.

**Haplopappus greenei.* Occasional, mostly above 1900 m. Hull, Bald Mt. (ne. Mendocino Co.), Black Butte, SYB, nNCR, KR, C.

Hazardia whitneyi (Gray) Greene var. *discoideus* (Howell) Clark (*Haplopappus w.* var. *d.* Howell). Occasional, above 1600 m. Hull, Black Butte, SYB, nNCR, KR, C.

Hieracium greenei. Rare, open red fir forest, 1850 m. St. John Mt., Hull, SYB, NYB, nNCR, KR, C, SN, T, P.

**Holodiscus boursieri.* Abundant, a subdominant shrub above 1550 m. Also on Goat Mt. Sanhedrin, Black Butte, Red Mt. (nw. Mendocino Co.), SYB, NYB, nNCR, KR, C, SN, T, P. The montane intermediates between coastal *H. discolor* and alpine *H. microphyllus* are taxonomically confused. We follow nomenclature of Munz (1959) for lack of a better alternative. Snow Mt. is the southernmost Coast Range locality for any of the montane intermediate forms.

**Horkelia tridentata* subsp. *flavescens.* Rare, ca. 1900 m. Sheetiron Mt., Sanhedrin, Hull, nw. Mendocino Co., SYB, NYB, KR, C, SN.

**Ipomopsis aggregata.* Rare, dry yellow pine forest, 1550 m. Black Butte, SYB, KR, C, SN.

**Ivesia gordonii.* Rare, scree, 2100 m. SYB, NYB, KR, C, SN.

Juncus howellii. Rare, wet meadow, 2010 m. Black Butte, SYB, KR, C, SN.

Kelloggia galioides. Occasional, above 1800 m. Reported from Cobb Mt. (Neilson, 1981). Sanhedrin, Hull, Black Butte, NYB, nNCR, KR, C, SN, T, P.

Lathyrus pauciflorus Fernald. Rare, 1750–1950 m. Sanhedrin, SYB, KR, C, SN.

**Leptodactylon pungens* subsp. *pulchriflorum.* Occasional, above 2000 m. St. John Mt., nNCR, KR, C, SN, T.

**Lesquerella occidentalis* subsp. *occidentalis.* Occasional, above 2100 m. Also on Goat Mt. Hull, SYB, NYB, KR, C, SN.

Lewisia nevadensis. Occasional, moist rocky flats, ca. 1950 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN, T.

Lewisia triphylla. Occasional, moist rocky flats, 1950–2050 m. Hull, Black Butte, SYB, KR, C, SN.

**Linanthus harknessii* var. *harknessii.* Reported by Brandegee (1893); no specimens nor living plants have been found. Black Butte (Plaskett Mdws. is the type locality of var. *condensatus*), SYB, KR, C, SN.

Linanthus rattanii. Type locality imprecise, possibly Snow Mt. Common, 1500–1600 m. Sanhedrin, Hull, Long Valley and Red Mt. (nw. Mendocino Co.), Black Butte, SYB.

Linum lewisii Pursh. Occasional, above 1850 m. Black Butte, SYB, NYB, KR, C, SN, T, P, north. Also in SCR, but at lower elevations. [*Jepson 13538,* cited by Jepson (Fl. Calif. 2:397) from Alameda Co., is *L. angustifolium.*]

Listera convallarioides. Rare, shaded seep, 1680 m. Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

Lithophragma glabra. Occasional, ca. 1950 m. Hull, Black Butte, NYB, KR, C, SN, T.

Lomatium ciliolatum var. *ciliolatum.* Common, above 1900 m. Also on Goat Mt. Sheetiron Mt., Hull, Black Butte, SYB, NYB, nNCR. Specimens from 1250 m and below in the Mt. Hamilton Range (SCR), annotated as this variety by Mathias and Constance, differ in their less compact compound leaves with narrower lobes; they lack the additional clusters of leaflets at the juncture of the opposite primary divisions that are especially conspicuous in NCR plants.

**Machaeranthera shastensis* var. *eradiata.* Occasional, above 1900 m. Hull, Black Butte, SYB, KR, C.

Melica bulbosa var. *bulbosa.* Rare, open red fir forest, 2090 m. Above Alder Springs, Black Butte, KR, C, SN. Variety *inflata* (=*M. bella* Piper) is quite distinct and occurs at lower elevations from Yolo to San Benito Cos. and in the Sierra Nevada.

Melica stricta. Rare, sheltered outcrops, 2075 m. Hull, Black Butte, SYB, NYB, KR, C, SN, T.

Microseris nutans. Occasional, above 1900 m. Longvale (nw. Mendocino Co.), nNCR, KR, C, SN.

**Mimulus breweri.* Common, wet meadow margins, above 1850 m. Sanhedrin, Hull, above Alder Springs, Black Butte, SYB, KR, C, SN, T, P.

Mimulus nanus. Occasional, above 2000 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN.

**Mimulus pilosellus* Greene (*M. primuloides* var. *p.*). Common, wet meadows, above 1850 m. Hull, Black Butte, SYB, NYB, KR, C, SN.

Monotropa hypopithys. Rare, oak-pine woods, 1350 m. Also at Pilot Grove Campground, 1200 m, 15 km sw. of Snow Mt. (*Hamann et al. s.n.,* in 1969). Sanhedrin, above Alder Springs, KR, C.

Muhlenbergia filiformis. Occasional, above 1900 m. SYB, NYB, KR, C, SN, T, P.

Osmorhiza occidentalis. Occasional, above 1700 m. Black Butte, SYB, KR, C, SN. *Purpus s.n.* (April 1898) from "Potter Valley, Mendocino Co." is likely from a higher elevation on Sanhedrin.

**Pedicularis semibarbata.* Common, above 1550 m, becoming abundant under red fir above 1900 m. Also on Cobb Mt. (*Baker 2179a*); reported from Bartlett Mt. (Brandegee, 1893) but not found by Howell (1946). Sanhedrin, Hull, Black Butte, nNCR, KR, C, SN, T, P.

Pellaea brachyptera. Occasional, outcrops and screes, above 1550 m. St. John Mt., Sanhedrin, Hull, nw. Mendocino Co., SYB, KR, C.

Penstemon purpusii. Type locality. Common, above 1700 m. Also on Goat Mt. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR.

Phacelia mutabilis. Occasional, open red fir forest, above 1900 m. Also on Goat Mt. and Cow Mt. [Sonoma Co. plants (*Heckard T-133*; see Heckard, 1960) are highly atypical and are more closely related to *P. nemoralis* Greene.] Sanhedrin, Black Butte, SYB, nNCR, KR, C, SN, P.

Phacelia procera. Rare, streamsides, above 1800 m. Hell's Half Acre (n. of Hull), Black Butte, SYB, KR, C, SN.

Phlox diffusa subsp. *diffusa.* Occasional, rocky flats, above 1950 m. Hull, Black Butte, SYB, KR, C, SN, T.

**Pinus jeffreyi.* Occasional, local, above 1550 m, sometimes in mixed stands with *P. ponderosa.* Many trees are unusually old and stunted. Hull, nw. Mendocino Co., SYB, NYB, nNCR, KR, C, SN, T, P. Also disjunct in se. San Benito Co.

Poa bolanderi. Rare, scree, 1950 m. Black Butte, SYB, KR, C, SN, T, P.

**Polygonum davisiae.* Rare, snowbed scree, 2135 m. Hull, SYB, KR, C, SN.

Polygonum kelloggii. Common, wet meadow margins, above 1900 m. Black Butte, SYB, NYB, KR, C, SN, T, P. Intergrading and confused with *P. confertiflorum,* which is widespread at lower elevations (including s. Lake Co.).

Polygonum minimum. Occasional, meadow margins, above 1850 m. SYB, NYB, KR, C, SN.

Polystichum scopulinum. Occasional, outcrops, 2075 m. Black Butte, SYB, NYB, KR, C, SN, T, P.

Potentilla drummondii. Rare, 1920 m. SYB, NYB, KR, C, SN.

Potentilla glandulosa subsp. *nevadensis.* Common, above 1800 m. Also on Goat Mt. Hull, above Alder Springs, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P.

**Purshia tridentata.* Occasional, as patches of old, gnarled, low and spreading shrubs, above 1950 m. Hull, KR, C, SN.

**Pyrola picta* var. *picta.* Occasional, above 1500 m. Also on Elk Mt. (*Tracy 2331*). Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

**Pyrrocoma apargioides* (Gray) Greene (*Haplopappus a.* Gray). Reported by Brandegee (1893); no specimen has been found. Only report for NCR: SN (Plumas Co. south) and adj. Nevada.

**Quercus vaccinifolia.* Occasional, dominant of shrubby thickets, 1950–2100 m. Sanhedrin, Hull, Black Butte, nw. Mendocino Co., SYB, nNCR, KR, C, SN.

**Raillardella scabrida* Eastwood. Type locality. Occasional, above 1950 m. Sanhedrin, Hull, SYB, NYB, nNCR.

**Ranunculus alismaefolius.* Occasional, moist rocky flats, 1950 m. KR, C, SN.

Ribes binominatum. Occasional, above 1800 m. Also on Goat Mt. Hull, Black Butte, SYB, NYB, nNCR, KR, C.

**Ribes lobbii.* Abundant, a subdominant shrub at 1850–2150 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, nNCR, KR, C.

Ribes nevadense. Rare, streamside under yellow pine, 1555 m. Sanhedrin, above Alder Springs, Black Butte, KR, C, SN, T, P.

Rorippa truncata (Jeps.) Stuckey. Occasional, wet meadows, 1830–1950 m. In California otherwise known from the shores of Clear L., Lake Co.; Lake Chabot, Solano Co.; and the San Gabriel and San Bernardino Mts.; widely but uncommonly distributed from the northern Rocky Mts. through the major river valleys of the central and western U.S. (Stuckey, 1972).

Sagina saginoides. Occasional, wet meadows, 1900–2050 m. Sheetiron Mt., Black Butte, SYB, NYB, KR, C, SN, T, P.

**Sedum obtusatum* subsp. *retusum.* Occasional, rocky places, 1500–1950 m. Also on Goat Mt. Sanhedrin (type locality), Black Butte, SYB, NYB, KR. Intergrades with subspp. *obtusatum* and *paradisum* Denton in KR.

Senecio triangularis. Occasional, above 1500 m. Sanhedrin, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P.

Sphenosciadium capitellatum. Occasional, 1575–1950 m. Reported from Cobb Mt. vicinity (Neilson, 1981). Black Butte, KR, C, SN, T, P.

Stephanomeria lactucina. Occasional, below 1600 m. Sanhedrin, Black Butte, SYB, KR, C, SN.

Stipa californica. Occasional, above 1800 m. Species limits in the difficult *S. occidentalis* lineage, of which this is a member, are currently under study by M. Barkworth (UTC). In California,

the entire lineage is predominantly Sierran, extending west to KR; otherwise known from NCR by single collections from Black Butte and SYB.

Thlaspi montanum L. var. *montanum.* Occasional, ca. 1750 m. Hull, Eden Valley (ne. Mendocino Co.), NYB, KR, C, SN.

Trifolium longipes. Occasional, 1550–1950 m. Sanhedrin, Hull, Sherwood Valley (ne. Mendocino Co.), Black Butte, SYB, KR, C, SN.

**Veratrum californicum.* Common, wet meadows, above 1750 m. Sanhedrin, Hull, nc. and ne. Mendocino Co., Black Butte, SYB, KR, C, SN, T, P.

Veronica serpyllifolia var. *humifusa.* Occasional, wet meadows, above 1500 m. Sheetiron Mt., Hull, Black Butte, SYB, KR, C, SN, T, P.

**Viola macloskeyi.* Occasional, wet meadows, above 1800 m. Hull, Black Butte, NYB, KR, C, SN, T, P.

**Viola purpurea* subsp. *integrifolia.* Common, above 1500 m; variable and not clearly separable from var. *purpurea* or from *V. quercetorum.* Also on Goat Mt. Sanhedrin, above Alder Springs, Black Butte, SYB, KR, C, SN. Baker (1949) cites Snow Mt. for both subsp. *purpurea* and subsp. *integrifolia,* the latter at its southern limit.

Discussion

Of the 128 taxa considered here to be at a margin of range, 43 were cited by Brandegee (1893) as basically Sierran (seven of these are now considered to belong to taxa not represented in SN). We have documented an additional 62 taxa that are characteristic of the Sierra Nevada, though their distributional centers are in some cases in the Klamath Mountains. Thus, 82% of the taxa listed are of Sierran affinity. Many, but not all, of these grow farther south in the Sierra Nevada than in the Coast Ranges.

Twenty-one other taxa are at the absolute southern margin of their ranges and are not found in the Sierra Nevada. Twelve of these are found spottily in the North Coast Ranges, are centered in the Klamath Mountains, extend east and usually north in the Cascades (sometimes as far south in the Cascades as n. Butte Co.). They are *Carex pachystachya, Collinsia torreyi* var. *latifolia, Eriogonum strictum* subsp. *proliferum, Fritillaria glauca, Galium sparsiflorum* subsp. *glabrius, Haplopappus greenei, Hazardia whitneyi* var. *discoideus, Machaeranthera shastensis* var. *eradiata, Monotropa hypopithys, Pellaea brachyptera, Ribes binominatum,* and *Ribes lobbii.* Five taxa (*Arabis* aff. *repanda, Arenaria nuttallii* subsp. *gregaria, Claytonia saxosa, Penstemon purpusii,* and *Sedum obtusatum* subsp. *retusum*) have been found only in the NCR and KR, and four are

endemic to the North Coast Ranges (*Epilobium nivium, Linanthus rattanii, Lomatium ciliolatum* var. *ciliolatum,* and *Raillardella scabrida*).

Two taxa are at the northernmost margin of California ranges on Snow Mt.: *Eriogonum nervulosum* (which is also endemic to the southern North Coast Ranges but is closely related to *E. ursinum* of KR, C, and SN) and *Rorippa truncata,* which has an unusually scattered distribution in North America east to the Mississippi River (Stuckey 1972).

Since Brandegee's (1893) initial documentation of "Sierra Nevada plants" in the high North Coast Ranges, the prevailing notion (e.g., Hulse-Stephens 1982) has been that members of these taxa have migrated north through the Sierra, west through the Cascade and Klamath Ranges, and south in the Coast Ranges to their current localities. We suspect that this explanation is based to some extent on a confusion between centers of population density and centers of origin.

There is considerable evidence that development of floras in California has been a coastward phenomenon, particularly regarding the forests. The general history of the middle and late Tertiary is one of increasingly continental and arid inland climates, with which successive waves of vegetation moved westward (Axelrod 1976, 1977; Raven and Axelrod 1978; Stebbins 1982). The direct evidence for these changes comes from fossil floras in which trees vastly predominate. Apparently, no such floras exist for northwestern California, including the entire Klamath Region. Hypotheses involving non-forest herbs and shrubs from that part of California, therefore, must rely on indirect evidence of other kinds.

Countering the general trend of coastward development of floras is evidence from the relative ages of the Klamath Region, the North Coast Ranges, and the Sierra Nevada. The Klamath Region, though derived from the same Nevadan (Late Jurassic) pluton as the Sierra Nevada, is the oldest continuously available land in the state, having been uplands of varying height (with several periods of uplift followed by erosion) throughout the Tertiary. Whittaker (1961) concluded that, because of its age and geological (including substrate) complexity, the Klamath Ranges are a floristic and vegetational center for the forests of much of the western United States. They are an important center for relictual endemic taxa (Stebbins and Major 1965), and no doubt have also provided stocks for outward migration and evolution, particularly during the climatic changes of the Tertiary. Both the North Coast Ranges and the Sierra Nevada are considerably younger as montane environments. The high NCR has apparently provided montane habitats since the end of the Miocene (Christensen 1966, Oakeshott 1971) but the Sierra Nevada was too low until Late Pliocene (ca. 12 million years ago) to produce a

strong rain shadow in western Nevada. Axelrod (1977, p. 149) calculated that the Mt. Reba flora in the Sierra Nevada has been uplifted about 1850 m since it was deposited in the Pliocene. Both NCR and SN had considerable mountain-building activity from Late Pliocene to mid-Pleistocene (Bateman and Wahrhaftig 1966, Christensen 1966, Oakeshott 1971). Thus, the order of appearance of montane habitats in these three major regions is Klamath Ranges, North Coast Ranges, and finally Sierra Nevada. For the plants of Klamath stock that currently occupy NCR and SN (probably the majority of taxa on our list), it seems reasonable to assume that populations have persisted in NCR for at least as long as in SN.

More work is needed to establish the relative magnitudes of these two countervailing effects, and we assume that both will prove to be important. Yet it is necessary to realize that many of these "Sierra Nevada plants" are likely to be relative latecomers to SN, regardless of their current relative population densities.

It is likely that the NCR endemics listed above arose mostly from Klamath Range stocks during the last half of the Tertiary under the influence of slowly changing climates. The small and interrupted ranges of some of them may indicate that extant populations are essentially relictual, having survived the more rapid fluctuations of the Late Pliocene and Pleistocene in localized pockets.

For most of the species at a margin of range on Snow Mt., it is no doubt the rapid decline in maximum elevation to the south that makes Snow Mt. their southern limit. Occurrence of many of these taxa in the mountains (including SN) of southern California is evidence that latitudinally determined climatic change is much less important than more local phenomena such as rain shadows and elevation. Because of the diversity of habitats occupied by the phytogeographically interesting taxa on Snow Mt., there is no single, precise answer to the question of why these taxa are never or rarely found farther south. Yet loss of appropriate habitats with declining maximum elevations is clearly the most general answer that can be posed.

Both the number (128) and the proportion (25%) of Snow Mt. plants at a margin of range are quite high (perhaps uniquely so) for such a small area. We know of no comparable data for regions in which the prevailing habitat type (general montane in this case) continues but a large proportion of the flora stops. However, under some circumstances (e.g., where mountains give way to desert), a similar or even larger proportion of the flora could be at a margin of range. Regardless of whether our use of superlatives is accurate, the flora of Snow Mt. is unique and will continue to instruct those who study it about the history and distribution patterns of California plants.

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